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Spatial patterns and density dependence in the dynamics of a roe deer (*Capreolus capreolus*) population in central Italy

Abstract The demography of roe deer living in a mountain area of central Italy was studied from 1995 to 1999 with 104 radio-tagged animals, including fawns and adults of both sexes. From spring surveys we estimated population density by mark-resighting (average: 53.8 ± 4.8 individuals km^{-2}) and found an average fawn/doe ratio of 0.75 ± 0.4. The fawn/doe ratio was negatively correlated to density suggesting density-dependent regulation in this population. Using culled and net-trapped individuals we evaluated the dressed body weights of adult males (23.1 ± 1.0 kg) and females (22.0 ± 1.0 kg), which indicated a low level of sexual dimorphism. The potential litter size (1.44 ± 0.1 embryos) depended on female body weight and a threshold of 20.9 ± 1.4 kg separated adult females carrying one or two embryos. Both fawn (0.38 ± 0.07) and adult survival (0.90 ± 0.07) were evaluated from radiotagged individuals and no gender effect was observed in either age class. During the study period we recorded a population decline in one part of the study area and an increasing fawn mortality, which was attributed to the spreading of an enteropathogenic desease. The study revealed an unexpected spatial structure in population dynamics at a scale of few square kilometres. In the two studied subareas, which are very close and ecologically similar, we documented significant differences in several demographic parameters: females in the subarea with the highest deer density produced smaller litters and allocated their reproductive effort preferentially to males, which is consistent with the hypothesis that local resource competition determines sex allocation in roe deer. The importance of spatial variability with respect to roe deer demography was overlooked in previous studies and our results raise new interesting research questions relative to the study of population equilibria which are also relevant for the management of this important game species.
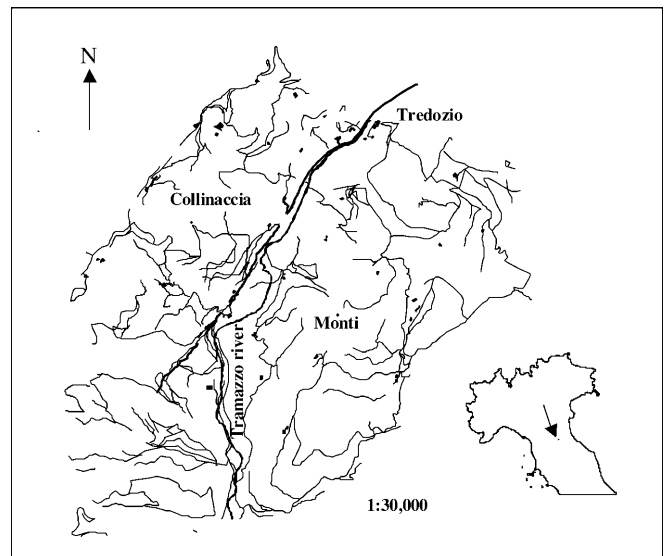
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Introduction

The vital rates of roe deer populations change as a function of several density-dependent and density-independent factors (Gaillard et al. 1998c), which determine their size and stability, i.e. the population equilibria. Density-dependent regulation of roe deer populations was described in southern Scandinavia (Liberg et al. 1997) and France (Vincent et al. 1995). Knowledge of the structure and regulatory mechanisms of roe deer populations is difficult to attain but it is of primary interest for the exploitation of this important game species in Europe (Cederlund et al. 1998).

Several studies have documented relevant fluctuations in the vital rates of roe deer populations (Gaillard et al. 1997) and correlation between vital rates and environmental (Latham et al. 1996) or climatic variables (Cederlund and Lindström 1983; Danilkin and Hewison 1996; Putman et al. 1996). In Britain, potential birth rate was reported to vary from 0.35 to 1.5, fawn survival from 0.27 to 0.75, and the autumn fawn/doe ratio from 0.14 to 0.84 (Ratcliffe and Mayle 1992). Adult survival appears to be less sensitive to external influences; in two populations in France, facing different environmental conditions, Gaillard et al. (1993) found very similar prime-age adult survival (about 0.85 for males and 0.95 for females).

The recent history of roe deer in Italy was summarised by Perco and Calò (1994). The removal of limiting factors of human origin after World War II, led to a fast increase in the species in the north-central mountain and hilly areas and thus, at the beginning of this decade, legal culling was allowed in the Apennines after a ban of 50 years. At that time no information was available on these populations and even the variation in simple demographic parameters is still poorly documented. In this study we first analysed vital rates, demographic parameters and density variations in a 5-year study.

Roe deer are characterised by a low sexual dimorphism. Under these conditions, we expect life-history traits, and in particular both fawn and adult survival, to be very similar in the two sexes. Neonatal survival of ungulates is strongly affected by predation (Linnell et al. 1995) and it is well known that foxes (*Vulpes vulpes*) prey upon roe fawns (Aanes et al. 1998). Despite the fact that in roe deer a sex-biased fawn survival was not observed (Gaillard et al. 1998c), the impact of fox predation seems to be larger on male than on female fawns (Aanes and Andersen 1996). Since in our study area both wolves and foxes are widely present, we expect *first,* that fawn survival should be lower than in other populations without large predators such as Chizé in France (Gaillard et al. 1993, 1997), Storfosna in Norway (Gaillard et al. 1998a) or in the Swabian mountains in Germany (Thor 1994) and *second,* that males should suffer lower survival when compared with female fawns. So we specifically tested whether, for fawns, male survival was lower than female survival.

While similar fawn survival in the two sexes is consistent with the low sexual dimorphism of the species, it is surprising that adult survival was lower in males than in females in many roe deer populations (Gaillard et al. 1998c and references therein). Thus, we tested the hypothesis of gender differences in adult survival.

Another potentially important source of variability for roe deer populations is spatial heterogeneity. To date, this point has received little attention and populations have generally been analysed under the assumption of panmixia within each study area. This assumption is quite unrealistic for roe deer, especially in situations such as the one studied here, where females exhibit strong philopatry, with home range sizes as small as 0.2 km² and almost complete overlapping of home ranges from year to year (Raganella Pelliccioni et al. 1998). Examples of the importance of short-scale spatial variations in the population dynamics of ungulates have been reported by Albon et al. (1997), who showed that the red deer (*Cervus elaphus*) population on Rum is composed of four groups with distinct dynamics, and by Coulson et al. (1999) for the Soay sheep (*Ovies aries*) on St. Kilda. Thus, the overall dynamics of the population may be strongly influenced by a complex network of interacting source-sink (sensu Pulliam and Danielson 1991) subpopulations. Such a situation was observed in northern Sweden where "roe deer rely more on immigration than on their own recruitment to avoid extinction" (Liberg et al. 1997). In this paper we systematically analyse spatial differences in vital rates and demographic parameters within the same population during the first 5 years of study. More specifically we test the hypothesis that a small-scale spatial structure exists in roe deer, characterised by relevant differences in dynamics as previously shown in other ungulates.

Finally we analysed the regulatory (feedback) mechanisms of this population via an analysis of correlation among demographic parameters. In the past, roe deer populations were thought to be regulated via social mechanisms (Strandgaard 1972), but more recently emphasis

was given to density-dependent regulation. In particular, several studies (Vincent et al. 1995; Boisaubert et al. 1997; Liberg et al. 1997) showed the effect of density on female productivity. Thus, we tested whether the studied demographic parameters were correlated to density.

Fig. 1 Study area of Tredozio (Province di Forlì-Cesena, Italy)

Materials and methods

Study area

The study area, located near the village of Tredozio (Fig. 1), in the northern Apennines (11°44′30″E, 44°04′37″N), is a private hunting estate in the Province of Forlì-Cesena and lies along an altitudinal range of 350–980 m a.s.l.; it is rich in water and characterised by the presence of woods and clearings, agricultural land and set-aside fields. The natural forest is made up of mixed forest stands mostly including oak (*Quercus cerris*, *Q. pubescens*) hophornbeam (*Ostrya carpinifolia*) and chestnut (*Castanea sativa*) and a few artificial plantations of conifers. The climate is sub-Mediterranean with an total annual precipitation of 810 mm, mostly in autumn, a mean annual temperature of 12.3°C, the hottest month being July (27.5°C), and the coldest one January (2.2°C) (data 1995–1998, from the ARPA Regional Metereological Service, Emilia Romagna). Snow cover occurs mainly in December and January and is usually slight and short-lived.

The study area is divided into two subareas – Collinaccia and Monti – of 1.82 km² and 2.43 km², respectively, separated by a paved road and a river which do not represent a strong barrier to animal movement. However, based on observations of radiocollared roe deer, the exchange between the two subareas appeared to be low, as very few individuals moved between them. The two subareas are ecologically comparable, but there are differences in the spatial arrangement of vegetation types, with a different extent and level of fragmentation of the forest stands. Despite the fact that we caught all the studied animals within these two subzones, subsequently some of them moved outside.

Captures and radiotagging

Adults and >6-month-old fawns were net-trapped in winter (January and February). Animals were weighed, sexed and fitted with

numbered radiocollars (TXE3, Televilt, Sweden); their age was assessed by tooth eruption criteria. We distinguished between only three age classes: newborns, 9-month-old fawns and older deer (adults). Newborn fawns were captured during the hiding period in May and June. They were weighed, sexed and individually marked with one small numbered eartag and an expandable radiocollar (TXH2, Televilt); their age in days was assessed on the basis of the appearance of the umbilical cord and behaviour during capture and handling (Jullien et al. 1992). All fitted radiocollars were provided with a mortality sensor; fawns were checked daily for mortality during summer, while adults were checked every 2 days.

From 26 May 1995 to 1 June 1999 a total of 104 roe deer were captured and radiocollared; 37 males and 20 females were captured as newborns, 11 males and 9 females were captured as fawns but at an age of >6 months, 20 females and 7 males were captured as adults. For net-trapped deer no capture-related mortality was recorded, since none died within 15 days following capture, while no effect due to the fitted radiocollar on fawn mortality was assumed (Garrott et al. 1985). When possible, the carcasses of radiocollared animals (32 fawns collared as newborns and 13 adults) were located and examined to assess causes of mortality.

Culling

Radiocollared animals were not culled. Stalking was carried out during summer for >1-year-old males, while females (>6 months old) were shot in January and February, when it was possible to assess numbers and, in most cases, sex of embryos. Dressed carcasses were weighed and aged.

Estimate of population density

Standard surveys were performed during the last week of March from 1995 to 1999. Surveys from vantage points (sensu Ratcliffe and Mayle 1992), available in most of the open areas, were performed in each subarea independently, in four consecutive, 2-h sessions at dawn and dusk. Population size was estimated by mark-resight using the software Noremark (White 1996). The joint hypergeometric maximum likelihood estimator (JHE) was used, on the assumption that the population is closed (White and Garrott 1990); in fact the movement of radio-tagged animals in and out the study area was negligible during each survey. Radiocollared animals were checked for their presence in the area of the count and, when present, they were computed in the population even when not directly seen (Eberhardt 1990). The use of other estimators such as the Minta-Mangel estimator (Minta and Mangel 1989), which relaxes the assumption of identical resighting probability, gave consistent results. The number of animals seen (minimum number alive, MNA) during each survey was also computed globally and per sex and age class. From MNA values we also derived the spring fawn/doe ratio (when fawns are about 9 months old) and the sex ratio of both subadults and adults.

In 1995 and 1996 a sufficient number of radiocollared roe deer were present only at Collinaccia, while, from 1997, JHE density estimates were computed for both subareas. The years 1995, 1996 (when radiotagged animals were available only at Collinaccia) and 1997, 1998 (when radiotagged animals were available in both subareas) were denoted as periods 1 and 2, respectively.

Data analysis

According to the species' life cycle, a roe deer cohort included all the individuals born in a given spring, usually from 25 May to 10 June at Tredozio. Because births were well clustered around 1 June the roe deer year i was defined as running from 1 June of the year i to 31 May of the year $i+1$. All fawns born in the spring of year i were included in the cohort of year i.

Survival rates were calculated from radiomarked individuals using the Kaplan and Meier estimator (Kaplan and Meier 1958), which fits better than other methods to the data of radiotracking studies since not all the animals are marked simultaneously (White and Garrott 1990).

For each year, 3 kinds of data sets were established to compute survival:

1. Animals marked as newborns in May and June. In order to have only right-censored data the birth date was manipulated so that all animals appeared to be born on 1 June. These animals were tracked for a maximum of 14 months but only the survival during the first year of life (12 months) was considered. Since fawns were captured at different ages (0–15 days) we tested for bias on annual survival estimates arising from heterogeneity in the age at capture by a rank-test for covariates (SAS Institute 1988a).
2. Animals of known age (i.e. captured as fawns or during their first winter of life). This data set is similar to the previous one but some animals of this group were followed for about 3.5 years (i.e. for the maximal duration of the TXE3 collars). These data were left- and right-censored.
3. Adults whose exact age may not be known. These data were left- and right-censored and one animal may be present in the data sets of different years. An animal may become part of this group because, while captured as a fawn, it became adult on its first birthday or because it was captured as an adult.

The data sets (1) and (2) relative to the different years are statistically independent because they include different individuals, while in data set (3) there are intraindividual replicates since one animal can be present in 2 different years. As well, when adult and fawn survival were compared, there were some animals present in both groups. Despite the fact that intraindividual replicates concern only some individuals in the sample (the mean presence of an adult in the sample was 2.3±0.14 years), we decided to account for this problem by reducing the chance of a type II error by using a lower probability threshold (0.01 and not 0.05) to indicate a significant result. For data set (3), sample size refers to the number of roe deer/year.

For two-sample survival tests, we used both left- and right-censored data, adopting the χ^2-test implemented in the SAS program by White and Garrott (1990). As this method did not allow for multiple comparisons, we used the non-parametric statistics implemented by the PROC LIFETEST (SAS Institute 1988a) when pertinent. This procedure manages only right-censored data so that we could apply it only to data set (1). Two survival curves may differ: (1) in the final survival value, i.e. that attained at the end of the studied period, or (2) may exhibit different patterns by which a similar final survival value is attained, or (3) in both features. Two non-parametric tests were used: the log-rank test, which is more sensitive to differences in longer survival time, case (1) above, and the Wilcoxon test that places more weight on early survival times, case (2) above. Of course, when both tests are significant the two survival curves are globally different [case (3)]. The comparison of the two tests allowed us to examine which parts of the survival curves were more different among strata.

For density, we reported mean and confidence interval because confidence limits are not symmetrical, since a log-normal distribution is assumed (Buckland et al. 1993, p 89); for other parameters, we reported mean±95% SE. The sex ratio $p = \frac{m}{m+f}$, where m and f are the number of males and females, respectively, was associated with a binomial SE, $1.95\sqrt{\frac{p(1-p)}{m+f}}$. For the spring fawn/doe ratio it was not possible to compute any SE (per year and subarea) because it was derived from MNA values of adult females and fawns.

Density dependence was assessed by Pearson correlation, after evaluation of the normality of the distributions of both density and vital rates tested, using the Wilks-Shapiro test (PROC UNIVARIATE of SAS).

All statistics were computed with SAS (SAS Institute 1988b) except binomial test (expected proportion 0.5), computed by

Table 1 The means for relevant demographic parameters are given by area and year. For each parameter or group of parameters we report the sample size. The minimum number of animals observed during spring counts was reported as sample size for all parameters estimated from those counts. Population density was estimated using the joint hypergeometric maximum likelihood estimator. The sample size of the birth sex ratio had to be computed by pooling sample sizes of sexed embryos and captured fawns [data set (1)]; captured fawns were also used to estimate fawn survival. Adult survival was computed using data set (3) (i.e. adults whose exact age may not be known)

Year	Data derived from spring counts					Data derived from culled females		Data derived from radiocollared deer				
	Density (deer/km²)	Fawn/doe ratio	Sex ratio			Embryos/ female	No. embryos	Fawn survival	No fawns	Sex ratio at birth	Adult survival	No. adults
			At 8 months	Adults	Minimum number alive							
Collinaccia												
1995		0.88	0.36±0.14	0.41±0.11	120			0.69±0.19	7	0.57±0.36	1ᵃ	14
1996	73.5 (66.4–86.5)	0.88	0.57±0.15	0.28±0.11	113	1.33±0.33	12	0.50±0.14	14	0.60±0.21	0.84±0.16	23
1997	63.1 (62.1–67.6)	0.53	0.44±0.19	0.39±0.10	113	1.33±0.42	8	0.42±0.22	7	0.80±0.17	0.85±0.17	24
1998	58.2 (53.2–70.3)	0.57	0.45±0.22	0.41±0.12	92	1.00±0.32	5	0.24±0.14	12	0.67±0.24	0.91±0.1	23
1999	42.3 (38.4–49.9)	0.77	0.50±0.20	0.37±0.13	69	1.33±0.33	8			0.88±0.23		
	59.3±6.5ᵇ	0.73±0.5ᵇ	0.46±0.08	0.38±0.05	101.4±9.4ᵇ	1.27±0.17	33	0.44±0.09	40	0.68±0.05	0.88±0.08ᵇ	84
Monti												
1995		1.00	0.53±0.15	0.49±0.11	129							
1996		0.81	0.48±0.19	0.55±0.12	95	1.56±0.24	14			0.33±0.37		
1997	42.3 (35.6–50.4)	0.73	0.47±0.22	0.51±0.13	77	1.50±0.37	12	0.17±0.11	13	0.65±0.18	0.92±0.1	13
1998	57.5 (41.6–86.4)	0.31	0.40±0.3	0.44±0.13	75	1.80±0.20	9	0.50±0.25	4	0.42±0.28	1ᵃ	13
1999	39.4 (37.6–42.4)	0.94	0.50±0.17	0.38±0.12	94	1.75±0.25	7			0.43±0.36		
	46.4±5.6ᵇ	0.77±0.7ᵇ	0.49±0.09	0.48±0.05	94.0±9.7ᵇ	1.61±0.12	42	0.25±0.1/1	17	0.51±0.08	0.93±0.08ᵇ	26
Study area	53.8±4.8ᶜ	0.75±0.4ᶜ	0.48±0.06	0.43±0.04	97.7±6.5ᶜ	1.44±0.10	75	0.38±0.07	57	0.61±0.05	0.90±0.07ᶜ	110

ᵃ All animals had the same fate and there was no censoring

ᵇ The SE accounts only for temporal variability

ᶜ The SE accounts only for between-area and temporal variability

SPSS 8.0 (SPSS 1998). Trends were computed by PROC REG of SAS. Other tests used were non-parametric (Spearman correlation, Wilcoxon two-sample test, Kruskal-Wallis ANOVA implemented by PROC CORR and PROC NPAR1WAY of SAS, respectively). We do not report df if 1. Two-way frequency tables were analysed by χ^2-test, while Fisher's exact test was reserved for small samples (PROC FREQ of SAS). We used probit regression to evaluate the effect of female body weight on the number of embryos carried (PROC PROBIT of SAS). Probit analysis is pertinent to compute a dose-response curve and to evaluate the threshold corresponding to a probability of 0.5. The relationship between sex ratio of embryos with maternal body weight and potential litter size was analysed by logistic regression (PROC LOGISTIC of SAS).

Results

Comparison of subareas

Population density, productivity and sex ratio

The estimates of density were more precise at Collinaccia [average coefficient of variation (CV)=0.11, $n=4$] than at Monti (average CV=0.21, $n=3$) (Table 1). This probably depended on both the smaller number of radio-tagged animals and the smaller probability of sightings at Monti. JHE population density at Collinaccia ($n=4$) was higher than at Monti ($n=3$; $z=4.8$, $P<0.001$). Density significantly decreased at Collinaccia (MNA, $F_{1,4}=18.9$, $P=0.02$; JHE, $F_{1,3}=46.3$, $P=0.02$) at a rate of 16.5% per year, but not at Monti (MNA, $F_{1,4}=2.3$, $P=0.22$; JHE, $F_{1,3}=0.02$, $P=0.9$).

The number of embryos per female remained constant among years in both sub-areas (Collinaccia, $\chi^2_3=2.1$, $P=0.56$; Monti, $\chi^2_3=0.05$, $P=1$; Table 1) but females were more productive at Monti than at Collinaccia (Wilcoxon test, $z=-2.5$, $P=0.01$), while there was no between-area difference in the fawn/doe ratio (Wilcoxon test, $z=0.42$, $P=0.67$; Table 1).

The sex ratios at birth computed: (1) using the number of sexed embryos, and (2) the number of captured newborns were strictly consistent (Collinaccia, $\chi^2=0.09$, $P=0.76$; Monti, $\chi^2=0.08$, $P=0.8$; overall $\chi^2=0.02$, $P=0.9$) in period 2, when both sub-areas were sampled. This result strongly suggested that fawn capture was not sex-biased and allowed us to use pooled data (embryos+newborns) to evaluate the sex ratio at birth (Table 1).

The evolution of the sex ratio in relation to animal age was not the same in the two subareas (Fig. 2). The sex ratio at birth exhibited a significant departure from the expected 0.5 value at Collinaccia (binomial test, $P=0.001$) but not at Monti (binomial test, $P=0.78$). There was a between-sub-area difference at birth ($\chi^2=3.7$, $P=0.05$) and at the adult stage ($\chi^2=6.3$, $P=0.01$), but not at 9 months ($\chi^2=0.21$, $P=0.64$). At Monti the sex ratio was similar among life stages while at Collinaccia the variation was large, with a strong male bias at birth but with a female-dominated population of adults. This decrease in the male segment of the population was highly significant at Collinaccia ($\chi^2_3=18.9$, $P<0.001$) but not at Monti ($\chi^2_3=2$, $P=0.57$).

Survival and causes of death

Fawn survival tended to decrease from period 1 (0.57 ± 0.12, $n=21$) to period 2 (0.3 ± 0.12, $n=19$) at Collinaccia (Wilcoxon test $\chi^2=3.8$, $P=0.05$; log rank test, $\chi^2=3.3$, $P=0.07$; Fig. 3) but the same survival curve was observed in both subareas in period 2 (Collinaccia, 0.3 ± 0.12, $n=19$; Monti, 0.25 ± 0.11, $n=17$; Wilcoxon test $\chi^2=0.16$, $P=0.7$; log rank test, $\chi^2=0.1$, $P=0.77$).

Overall our data did not reveal between-sex differences in fawn survival (0.38 ± 0.07, $n=21$, Wilcoxon test $\chi^2=0.78$, $P=0.38$, log rank test, $\chi^2=0.9$, $P=0.34$). Comparing sex-specific survivals (period 2), we found a large difference, albeit not quite significant, at Monti (females, 0.44 ± 0.18, $n=8$; males, 0.11 ± 0.1, $n=9$; Wilcoxon test $\chi^2=3.5$, $P=0.06$; log rank test $\chi^2=3.3$, $P=0.07$) but not at Collinaccia during the same period (females, 0.25 ± 0.22, $n=4$; males, 0.35 ± 0.14, $n=15$; Wilcoxon test $\chi^2=1$, $P=0.32$; log rank test, $\chi^2=1.2$, $P=0.27$) or during period 1 (females, 0.69 ± 0.19, $n=8$; males, 0.5 ± 0.14, $n=13$; Wilcoxon test $\chi^2=0.58$, $P=0.45$; log rank test, $\chi^2=0.62$, $P=0.43$).

Survival was higher for adults [data set (3)] than for fawns [data set (2)], both in general (adults, 0.89 ± 0.06, $n=118$; fawns, 0.21 ± 0.19, $n=78$; $\chi^2=52.2$, $P<0.001$), and when the two sub-areas were considered separately (Collinaccia, adults, 0.88 ± 0.08, $n=84$; fawns, 0.39 ± 0.18. $n=52$; $\chi^2=25.2$, $P<0.001$; Monti, adults, 0.93 ± 0.08, $n=34$; fawns, 0.2 ± 0.19, $n=18$; $\chi^2=26.7$, $P<0.001$), while there was no between-area difference in survival rates when the same age classes were compared (period 2, fawns, $\chi^2=0.025$, $P=0.87$; adults, $\chi^2=1.02$, $P=0.31$).

Since there was no significant difference in mortality causes either between adults and fawns (Fisher's exact test, $P=0.6$) or between the two subareas (Fisher's exact test, $P=0.13$), data were pooled: predation accounted for 37.8%, diseases for 17.8% and human activities for 20% of casualties. It was not possible to determine precisely the cause of death in 24.4% of cases.

Body weight

A between-sex comparison of body weights from winter captures revealed no significant sexual dimorphism
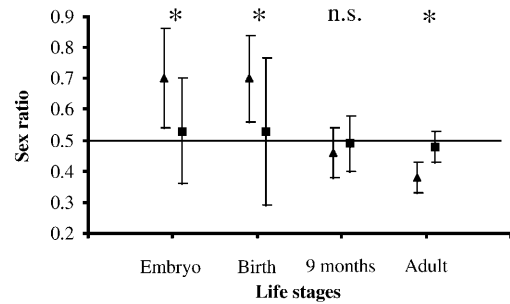
Fig. 2 The sex ratio is plotted as a function of four different life stages at Collinaccia (s) and Monti (n). *$P<0.05$, $n.s.$ $P>0.05$
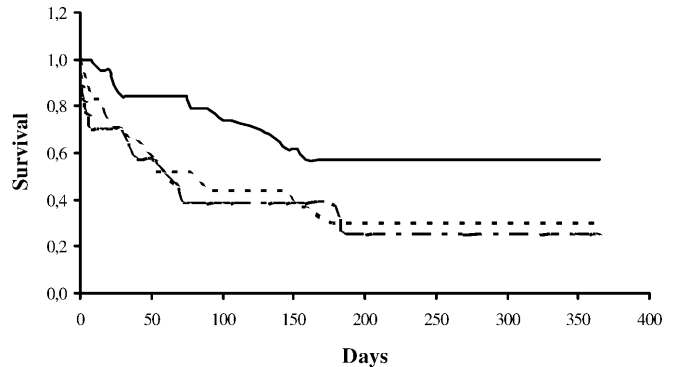
Fig. 3 Comparison between fawn survival at Collinaccia in period 1 (*continuous line*, $n=21$), at Collinaccia in period 2 (*dashed line*, $n=19$) and at Monti in period 2 (*dashed and dotted line*, $n=17$)

(>6-month-old fawns: females, 16.0 ± 1.3 kg, $n=24$; males, 16.1 ± 1.3 kg, $n=10$, ANOVA, $F=0.01$, $P=0.91$; adults: females, 22.1 ± 1 kg, $n=82$; males, 23.1 ± 3.9 kg, $n=13$). Body weight was not significantly different in the two subareas (Collinaccia, 20.7 ± 0.96 kg; Monti, 22.1 ± 0.86 kg; ANOVA, $F=3.2$, $P=0.08$). Among sex and age classes, the largest difference was observed for female fawns (Collinaccia, 15.3 ± 1.14 kg, $n=15$; Monti, 17.2 ± 2.8 kg, $n=9$; ANOVA $F=2.23$, $P=0.14$).
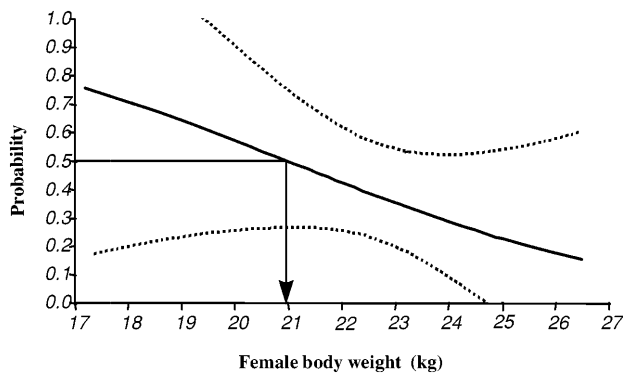
Population regulation

Female body weight and vital rates

The sex ratio at birth was negatively correlated with female body weight (Spearman correlation, $r=-0.89$, $n=6$, $P=0.02$), while the fawn/doe ratio was positively related to female body weight of the winter of previous year (Spearman correlation, $r=0.75$, $n=7$, $P=0.05$) (Fig. 4).

The previous analysis was complemented by analyses of individual data. To understand the role of maternal body weight with respect to the number of embryos, we computed the probit regression curves to detect possible thresholds for the production of 0 vs. 1 and 1 vs. 2 embryos. There was no significant probit regression be-
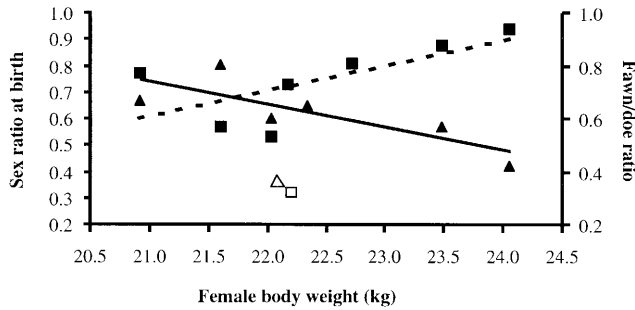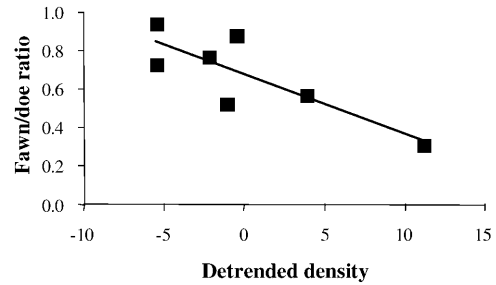
Fig. 4 The sex ratio at birth (s) and the spring fawn/doe ratio (n?) are plotted as functions of dressed body weight of adult females, estimated in the winter preceding birth; Δ and q refer to outliers which were not used for the computation of correlations. Both outliers were observed at Monti: Δ refers to sex ratio in 1996, when the sample size was too small (three females) to be reliable, while q refers to a very low fawn/doe ratio in 1997, linked to the exceptional mortality of male fawns in the same year (see text for further explanation)

Fig. 6 Correlation between fawn/doe ratio and detrended density

gression was significant ($\chi^2_2 = 8.2$, $P=0.02$, $n=38$), but the effect of the number of embryos ($\chi^2=7.02$, regression coefficient $r=-1.8$, $P=0.008$) was more important than that of body weight ($\chi^2=0.06$, regression coefficient $r=-0.05$, $P=0.8$).

Density dependence

The fawn/doe ratio was negatively correlated with detrended density values (Pearson correlation coefficient, $r=-0.83$, $P=0.02$, $n=7$; Fig. 6). No other vital rates appeared to be correlated to detrended density (Pearson correlation coefficient; primary sex ratio, $r=-0.32$, $P=0.41$, $n=7$; fawn survival, $r=0.52$, $P=0.37$, $n=5$; litter size, $r=0.07$, $P=0.88$, $n=7$).

Fig. 5 Probit regression: dose-response curve (*continuous line*) and confidence limits (*dotted lines*) of litter size as a function of female body weight (*abscissae*). On the ordinates we report the probability of carrying one embryo. The *thin horizontal line* refers to a probability level equal to 0.5 and the *arrow* indicates the threshold, or dose 50%. Curves are limited to the ranges of body weights observed in this study. Confidence limits beyond the probability range 0–1 were not plotted

tween female weight and the probability of carrying 0 embryo ($\chi^2=0.67$, $P=0.41$, $n=24$); its critical threshold was located outside the range of observed weights with a very large confidence interval (14.7±8.84 kg). The second regression (Fig. 5), which analysed the threshold between 1 and 2 embryos, was much sharper (the regression being almost significant: $\chi^2=3.1$, $P=0.08$, $n=50$) indicating the presence of a 50% critical threshold at a body weight of 20.9±1.4 kg. The transition was fast: almost no adult female had 2 embryos if its weight was <20 kg and almost every female carried 2 embryos if its weight exceeded 23 kg. Using a probit model with multiple levels (0, 1, 2 and 3 embryos) the effect of body weight was significant ($\chi^2=4.3$, $P=0.04$, $n=56$).

We used a logistic regression to highlight the relationships between sex ratio of embryos with both maternal body weight and potential litter size. The multiple re-

Discussion

The dynamics of the roe deer population of Tredozio appeared to be more complex than we believed at the onset of this study. The following main conclusions emerged from this study: (1) a clear spatial structure of this roe deer population, (2) a higher variability of fawn survival with respect to adult survival, (3) a crucial role of female body weight in relation to the allocation of reproductive effort, (4) density-dependent regulation.

We confirmed the stability of adult survival when compared to fawn survival (Gaillard et al. 1998b). According to the low sexual dimorphism of this population, we did not observe a gender effect on survival except for the extremely low survival of male fawns at Monti in 1997. Adult survival was similar to that described in a previous study in comparable environments (Gaillard et al. 1993). In contrast with other findings on roe deer populations [see Gaillard et al. (1998c) for a review], we did not detect any differences in adult survival between the two sexes. Anyway, more data are needed to clarify the possible existence of reduced survival of bucks at Tredozio.

As expected, in our study area predation accounted for most population losses, both for adults and fawns. Since adult survival was high and similar to that observed in comparable sites without large predators

(Gaillard et al. 1993), we may assume a weak effect of predation on this age class. Nothing can be concluded about the effect of predation on fawns since their mortality seems to be subject to density-dependent regulation (Gaillard et al. 1997). We believe that it might be interesting to test the impact of predation upon fawn survival (compensatory vs. additive effects) by fox-removal experiments.

An expected source of mortality which might explain the observed population decline at Collinaccia, and the high fawn mortality observed at Monti in 1997, was the spread (recorded for the first time in spring 1997) of an epidemic caused by an enteropathogenic strain of *Escherichia coli* (O:79) which touched a much wider region than our study area. Adult lethality, estimated from radiocollared deer, was around 80%, with a global mortality of 10%; its impact on newborns is unknown, but it is likely to be severe (Guberti et al. 1999). It is clear that many differences observed between period 1 (before the onset of the epidemics) and period 2 might be influenced by this disease.

The potential litter size of female roe deer at Tredozio was similar to that described in other populations (Hewison 1996; Liberg et al. 1997). In roe deer, the sex ratio was found to be increasingly male biased as average maternal body weight decreased (Hewison and Gaillard 1996). Our findings are consistent with this theory since lighter does produced more males and the sex ratio was subject to density dependence resulting in male-biased production at Collinaccia, where the density was highest. Interestingly, the relationship between sex ratio and body weight seems to be indirect, via the effect of body weight on potential litter size. A threshold exists in body weight in relation to the number of implanted embryos. A relationship between body weight and potential litter size was found by Mauget et al. (1999) who observed that those carrying twins were heavier than those carrying singletons. The relationships found suggested that the years characterised by a large male production caused a low recruitment in the population (i.e. the population dynamics seems to be dominated by female-biased years). Unfortunately, we could not refine our characterisation of the potential productivity of this population because we could not distinguish reliably second year does from prime age animals, considering the former are often characterised by a lower productivity (Danilkin and Hewison 1996; Hewison 1996). In addition, we could not determine the percentage of second year does which reproduced.

The spring fawn/doe ratio was <1. Similar values were observed by Ratcliffe and Mayle (1992), Strandgaard (1972) and Krämer (1994). Vincent et al. (1995) showed that an autumn ratio >1 is typical of low-density populations while ratios <1 occurred at high density. Fawn/doe ratios are the product of litter size and fawn survival. Both litter size (Liberg et al. 1997) and fawn survival (Gaillard et al. 1997) may exhibit density dependence. Also this Apennine population appeared to be subject to density-dependent regulation of the fawn/doe ratio. It is relevant to point out the importance of female body weight in the population dynamics of roe deer.

A new and interesting finding of this work is the existence of short-scale demographic variations. Coulson et al. (1999) developed a complex statistical approach in order to identify a suitable scale for the analysis of the demography of subpopulations. In our case the choice to analyse Collinaccia and Monti data separately was quite natural due to the topography of the study area. Gaillard et al. (1998a) showed that there are differences of growth and survival at the family level, i.e. at a scale of "one home range", while the differences described by this work referred to a larger spatial scale of "several home ranges". These spatial structures are much smaller than the scale at which roe deer populations are usually studied. Although both subareas were characterised by similar habitats (Carnevali 1998), shared the same management and are very close, vital rates were very different: at Collinaccia the population seemed close to carrying capacity while at Monti the potential increase seemed higher. Of course, it is possible that this situation was determined by unknown events occurring before the onset of this study. However, results suggested to us that it would be worth looking for spatial heterogeneity in roe deer demography. The presence of spatial structuring raises two interesting research questions: (1) what are the biological mechanisms which maintain these differences over the long term and, (2) what impact do these differences have on the population dynamics at a large scale?

We may wonder why in this population females do not compensate for such a fitness difference, by moving from one area to the other, i.e. from Collinaccia to Monti, such as Wahlström and Kjellander (1995) observed in Sweden. The reduced movement between the two subareas and the strong philopatry of adult females may account for the lack of demographic synchrony and this implies a high cost of shifting. However, even with a reduced dispersal rate we expect that, in the long term, the two subareas would attain similar population densities.

It may be conjectured that heterogeneity arises from the sharp non-linearity of the relationship linking litter size and female body weight. Studies of ungulate demography assume progressive and smooth density effects (it is usual to use linear correlation, as we did, to detect density dependence). However, due to the threshold effect described in this paper, even small reductions of female body weight may produce a sharp fall in litter size and hence in recruitment. In other words, the stock-recruitment function for roe deer may not be purely compensatory (e.g. a Beverton-Holt function) but might be overcompensatory (e.g. a Ricker function). It is well known [cf. Caswell (1989) and references therein] that overcompensation may lead to the disappearance of a stable equilibrium which is replaced by a quasi-periodic solution (Hopf bifurcation). Chesson (1998) clearly showed that when populations are spatially structured and the stock-recruitment function is Ricker's, predictions derived from the average population are incorrect. Thus, the presence

of a spatial structure in population dynamics is also of high importance for roe deer management.

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